AGU PUBLICATIONS

JGR

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE
10.1002/2017JG004135

Key Points:
- Environmental perturbations can stress ecosystems and reduce their resilience causing them to cross a critical transition
- The cumulative influences of fires within our study catchment drive an abrupt transition in the lake diatom community at ca. 820 cal yr BP
- Increased variability and system state shifts precede critical transitions indicating there are measurable early warning signals at our site

Supporting Information:
- Supporting Information S1

Correspondence to:
K. K. Beck,
beckk@student.unimelb.edu.au

Citation:
Beck, K. K., Fletcher, M.-S., Gadd, P. S., Heijnis, H., Saunders, K. M., Simpson, G. L., & Zawadzki, A. (2018). Variance and rate-of-change as early warning signals for a critical transition in an aquatic ecosystem state: A test case from Tasmania, Australia. *Journal of Geophysical Research: Biogeosciences*, *123*, 495–508. https://doi.org/10.1002/2017JG004135

Received 28 AUG 2017
Accepted 28 JAN 2018
Accepted article online 7 FEB 2018
Published online 21 FEB 2018
Corrected 2 APR 2018

This article was corrected on 2 APR 2018. See the end of the full text for details.

Variance and Rate-of-Change as Early Warning Signals for a Critical Transition in an Aquatic Ecosystem State: A Test Case From Tasmania, Australia

Kristen K. Beck[1], Michael-Shawn Fletcher[1], Patricia S. Gadd[2], Henk Heijnis[2], Krystyna M. Saunders[2], Gavin L. Simpson[3], and Atun Zawadzki[2]

[1]School of Geography, University of Melbourne, Parkville, Victoria, Australia, [2]Australian Nuclear Science and Technology Organisation, Lucas Heights, New South Wales, Australia, [3]Institute of Environmental Change and Society, University of Regina, Regina, Saskatchewan, Canada

Abstract Critical transitions in ecosystem states are often sudden and unpredictable. Consequently, there is a concerted effort to identify measurable early warning signals (EWS) for these important events. Aquatic ecosystems provide an opportunity to observe critical transitions due to their high sensitivity and rapid response times. Using palaeoecological techniques, we can measure properties of time series data to determine if critical transitions are preceded by any measurable ecosystem metrics, that is, identify EWS. Using a suite of palaeoenvironmental data spanning the last 2,400 years (diatoms, pollen, geochemistry, and charcoal influx), we assess whether a critical transition in diatom community structure was preceded by measurable EWS. Lake Vera, in the temperate rain forest of western Tasmania, Australia, has a diatom community dominated by *Discostella stelligera* and undergoes an abrupt compositional shift at ca. 820 cal yr BP that is concomitant with increased fire disturbance of the local vegetation. This shift is manifest as a transition from less oligotrophic acidic diatom flora (*Achnanthidium minutissimum*, *Brachysira styriaca*, and *Fragilaria capucina*) to more oligotrophic acidic taxa (*Frustulia elongatissima*, *Eunotia diodon*, and *Gomphonema multiforme*). We observe a marked increase in compositional variance and rate-of-change prior to this critical transition, revealing these metrics are useful EWS in this system. Interestingly, vegetation remains complacent to fire disturbance until after the shift in the diatom community. Disturbance taxa invade and the vegetation system experiences an increase in both compositional variance and rate-of-change. These trends imply an approaching critical transition in the vegetation and the probable collapse of the local rain forest system.

1. Introduction

Environmental pressures or perturbations can erode the resilience of an ecosystem such that, in cases where multiple stable states exist, a threshold is crossed and the system shifts into a new stable state (Bunting et al., 2016; Carpenter & Brock, 2006; Wang et al., 2012). These critical transitions are a nonlinear ecosystem response to a change in conditions, such as nutrient influx, climate, and/or land use change (Lenton, 2011; Scheffer et al., 2001, 2009; Scheffer & Carpenter, 2003; Wang et al., 2012). Nonlinear ecosystem dynamics and the existence of multiple stable states have profound implications; as state transitions can be sudden and unpredictable. Once a state shift has occurred in response to a perturbation, internal feedbacks can "fix" the ecosystem in the new stable state irrespective of continued perturbation—i.e. hysteresis (Fletcher et al., 2014; Scheffer et al., 2009; Scheffer & Carpenter, 2003). Consequently, an important endeavor is the attempt to detect "early warning signals" (EWS) that precede critical transitions in nature (Dakos et al., 2015; Scheffer et al., 2009; Wang et al., 2012). While theory predicts that EWS should precede some types of critical transitions detecting these signals remains challenging, particularly for ecosystems with long generational timespans, such as temperate forests. Nevertheless, given the clear importance of critical transitions for ecosystem function and monitoring, considerable attention has been paid to theorizing and attempting to measure EWS to improve predictive power (Bunting et al., 2016; Carpenter & Brock, 2006; Dakos et al., 2015; Scheffer et al., 2009, 2012; Seddon et al., 2016; Wang et al., 2012).

Critical transitions are often preceded by a reduction in resilience, the ability of a system to both resist and recover from perturbations (Hodgson et al., 2015; Scheffer et al., 2009). These factors of lost resilience are associated with increased recovery time and variance, and a concerted effort has been made to measure these

components in an attempt to understand how resilience changes through time (Carpenter & Brock, 2006; Dakos et al., 2012; Scheffer et al., 2009). A slowdown in recovery time, as a system approaches a critical transition, is termed "critical slowing down" (Scheffer et al., 2009). It is this property that has received most attention when attempting to measure changes in resilience and detect EWS (Scheffer et al., 2009; Wang et al., 2012). During a critical slowing down, statistical properties of time series data can be quantified to measure an ecosystem state. Some examples of EWS include high autocorrelation at lag +1, increasing variance, and skewness (Dakos et al., 2015; Scheffer et al., 2009, 2012; Wang et al., 2012). Additionally, rate-of-change (ROC) can measure the change in state recovery for a critical transition, where increased ROC demonstrates an EWS of longer recovery and a loss in resilience (Lim & Epureanu, 2011). Despite a well-established theoretical underpinning, actual measurements of EWS in natural systems are few, particularly in ecology where species generational times often exceed observation windows, thus, precluding direct measurement. It is here that high-resolution palaeoecological data are an important tool for testing the concepts underlying EWS.

Palaeoecological data can be used in the absence of monitoring data to comprehend long-term ecosystem dynamics, allowing an understanding of how ecosystems change through time, and an appreciation of the factors that can cause critical transitions and the formation of new stable states (Fletcher, Wood, & Haberle, 2014; Wang et al., 2012; Willis et al., 2010). Importantly, palaeoecological data are rarely evenly spaced in time; thus, data are usually manipulated (often via interpolation) prior to application of many of the metrics of resilience, such as autocorrelation and skewness (e.g., Wang et al., 2012). Critically, the manipulation of time series data can unintentionally cause false correlations and remove important trends (Carstensen et al., 2013; Dakos et al., 2012; Schulz & Stattegger, 1997). In some cases, interpolation of data can artefactually cause an increase in standard deviation (i.e., variance), autocorrelation, and broadening of skew—all considered potential EWS that precede critical transitions (Carstensen et al., 2013). Thus, it is important to select appropriate metrics when using palaeoecological data to measure resilience and EWS. Variance, for example, has been a successfully employed measure for palaeoecological data without interpolation, allowing an effective test for EWS and critical transitions (Bunting et al., 2016; Dakos et al., 2012). In addition, ROC can be used to measure EWS, without interpolation, as an erosion of resilience before a critical transition (Scheffer et al., 2012; Siteur et al., 2016).

Here we use a suite of palaeoecological data to understand the interconnection between changes in vegetation, nutrient cycling, sediment delivery, and diatom community structure through time. Our study site is Lake Vera, southwest Tasmania, Australia, a mountainous cool temperate landscape in which fire activity exerts a major influence over terrestrial ecosystem dynamics. Importantly, little is known about how fire-driven landscape change in this region influences aquatic ecosystem dynamics. We present data on temporal changes in diatom community composition, lake sediment geochemistry, pollen, and charcoal spanning the last 2,400 years. Our objective is to test the response of the lentic ecosystem to changes in the local catchment. We specifically ask the following: (i) What is the response of the diatom community to fire-driven catchment change?; (ii) If changes in diatom community structure do occur, are they linear or nonlinear?; and (iii) Can we detect EWS for any abrupt aquatic ecosystem change (i.e., critical transitions)?

1.1. Biogeography of Tasmania

Tasmania (40–44°S) is a continental island that has a cool temperate maritime climate (Gentilli, 1971). The island is bisected by northwest-southeast trending mountain ranges that intercept the prevailing mid-latitude westerly airflow, resulting in a steep west to east orographic precipitation gradient. The steep topography and rainfall gradient results in two distinct bioclimatic regions: a dry (ca. 400 mm p/a) open *Eucalyptus*-dominant savanna in the east of Tasmania and a wet (up to 3,500 mm p/a) west where moorland and rain forest dominate (Fletcher & Thomas, 2010; Macphail, 1979). The uniformly nutrient poor bedrock (Jurassic dolerite) and hyperhumid climate of western Tasmania results in the development of predominantly acidic organosols under all vegetation types (Isbell, 2002; Pemberton, 1988, 1989). Lake characteristics also follow this biogeographic divide, with acidic, oligotrophic to dystrophic waters in the west and turbid, less acidic, (ultra)oligotrophic, saline lakes in the east (Tyler, 1974; Vanhoutte et al., 2004). Fire has shaped the regional vegetation of Tasmania. In the west, this has resulted in a failure of rain forest to occupy its climatic niche, and instead, the landscape is dominated by fire-promoting plant communities. Fires are climate-limited in the west, where biomass is uniformly high, with interannual shifts in the strength and position of the westerly winds the main control over fire activity (Mariani & Fletcher, 2016).

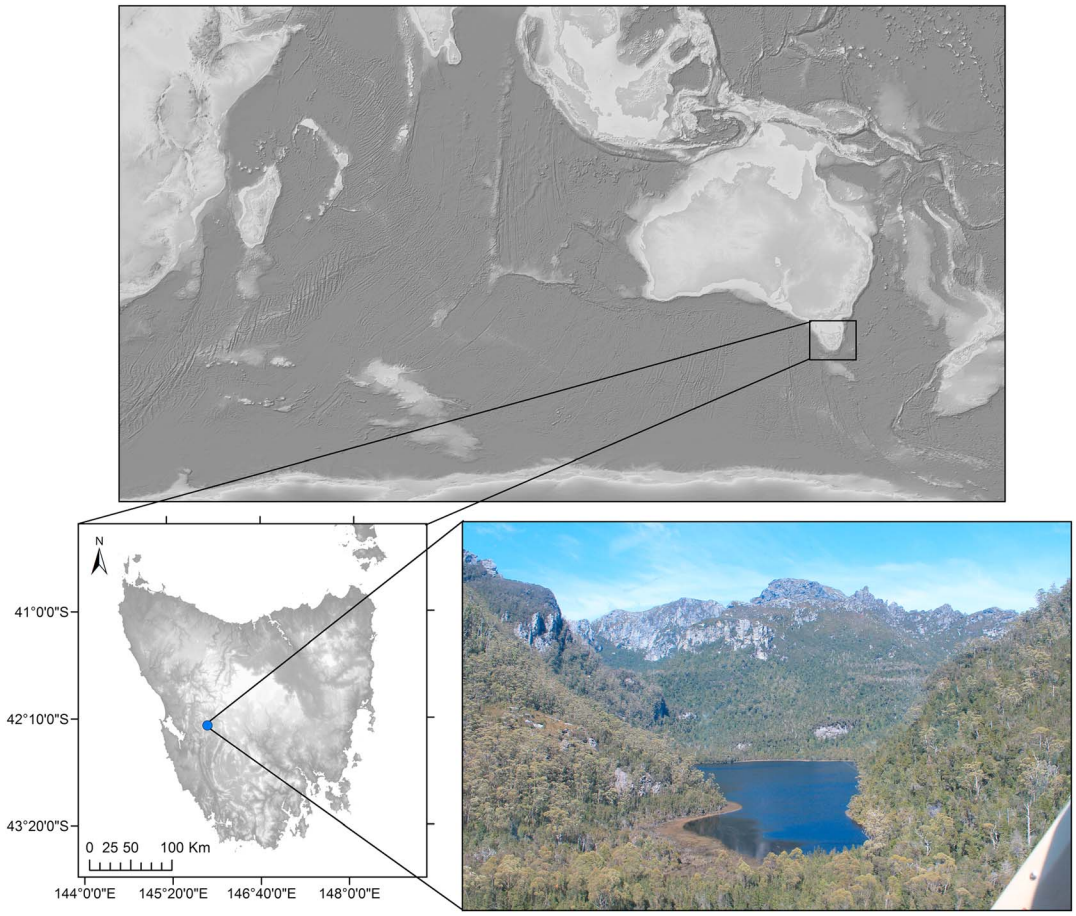

Figure 1. Map of Australia (top), inset map of Tasmania (left) with site location (blue dot), and a photo of Lake Vera, Tasmania (right).

1.2. Study Site

Lake Vera (42°16′29″S, 145°52′44″E) is a small moraine-bound lake formed in a glacial valley located near Frenchman's Cap, southwest Tasmania, Australia (Figure 1). The site lies within the region of strongest correlation between interannual shifts in the midlatitude westerlies and rainfall anomalies on Earth (Gillett et al., 2006; Hill et al., 2009). Lake Vera lies 550 masl, is dystrophic/oligotrophic and acidic with a maximum water depth of 48 m. Annual mean precipitation is ~2,800 mm and mean annual temperature is ~8.7°C (Bradbury, 1986; Macphail, 1979; Markgraf et al., 1986). Surrounding vegetation includes the following: rain forest and related scrubland, heathland complexes, wet eucalypt forest and woodland, and noneucalypt forest and woodland. Dominant taxa within the local catchment consist of *Atherosperma moschatum*, *Athrotaxis selaginoides*, *Eucryphia lucida*, *Eucalyptus delagetensis*, *Lagarostrobos franklinii*, *Leptospermum nitidium*, and *Nothofagus cunninghamii* (Department of Primary Industries, 2017; Fletcher et al., 2018; Kitchener & Harris, 2013). Catchment geology, while not well described, contains mainly siliceous glacial deposits (Bradbury, 1986; Macphail, 1979).

2. Materials and Methods

2.1. Coring and Chronology

In 2011 a 105 cm core (TAS1108 SC1) was collected from 48 m depth in Lake Vera using the Universal coring system (Aquatic Research Instruments, 2016). Radiometric analysis was performed at the Australian Nuclear Science and Technology Organization (five ^{210}Pb samples) and The National Ocean Sciences Accelerator Mass Spectrometry (four radiocarbon samples) (Table 1). All radiocarbon samples were bulk sediment

Table 1
Radiocarbon Results for Lake Vera, Including NOSAMS Laboratory Identification Number, Sample Depth (cm), Sample Type, the F Modern and Error, the Radiocarbon Age (BP) and Error (1σ), and $\delta^{13}C$ (per mil)

ID #	Depth (cm)	Sample type	F modern and error (1 σ)	Radiocarbon age and error	$\delta^{13}C$ (per mil)
OS-92421	23–23.5	Sediment organic carbon	0.9222 ± 0.0028	650 ± 25	−27.72
OS-92422	50–50.5	Sediment organic carbon	0.8543 ± 0.0034	1,260 ± 30	−27.6
OS-92423	81–81.5	Sediment organic carbon	0.7758 ± 0.0029	2,040 ± 30	−27.55
OS-89128	103.5–104	Sediment organic carbon	0.7423 ± 0.0025	2,390 ± 25	−27.15

Note. NOSAMS = National Ocean 145 Sciences Accelerator Mass Spectrometry.

dried in a convention oven, rootlets removed, and pretreated with HCl to remove of any carbonates. Radiocarbon dates were calibrated to calendar years with Southern Hemisphere calibration curve to 1 standard deviation—SHCal13 (Hogg et al., 2013). Samples for ^{210}Pb dating were chemically processed and analyzed by alpha spectrometry (Atahan et al., 2015). ^{210}Pb ages were determined using the constant initial concentration (CIC) ^{210}Pb dating model (Robbins & Edgington, 1975), which estimated a constant sediment accumulation rate of 0.009 g/cm^2/year, approximately 0.036 cm/year. ^{210}Pb ages were also calculated using the constant rate of supply model (Appleby & Oldfield, 1978) and were in good agreement with the CIC model ages down to 3 cm depth. Due to the deep anoxic nature of this lake, we would expect a relatively constant sediment accumulation rate throughout Lake Vera's history, and thus, the CIC model ^{210}Pb dates would be more appropriate to use for the age model (see supporting information). A Bayesian age-depth model was developed in R *v. 3.4.1* (R Development Core Team, 2014) using the Bacon *v. 2.2* package (Blaauw & Christen, 2013) (Figure 2).

2.2. Geochemical Analysis

Nondestructive geochemical data were obtained using an Itrax X-ray fluorescence (XRF) core scanner at Australian Nuclear Science and Technology Organization at a resolution of 0.2 mm using a molybdenum (Mo) tube set at 30 kV and 55 mA with a dwell time of 10s. The geochemical data (Fe, Mn, and Ti) were normalized by the Mo Incoherence/Coherence ratio (Croudace & Rothwell, 2015), and the Fe/Mn ratio was determined to demonstrate changes in redox conditions (Carignan & Tessier, 1988; Koinig et al., 2003; Kylander et al., 2011), alkalinity increases, and Fe richness with fire disturbance (Ketterings et al., 2000; Korhola et al., 1996). Fe oxides are released from soils into waterbodies with fire (Korhola et al., 1996) and become soluble ferrous Fe that preservers in lake sediments when met with anoxic waters (Cohen, 2003).

Analysis for the percent Carbon (C%) and Nitrogen (N%) was performed at 0.5 cm intervals with an average sampling resolution of ca. 12 cal yr BP. Samples were pretreated with 10% HCl, freeze-dried, and ground to create a homogeneous composition then analyzed at the University of Waterloo on a Carlo Erba Elemental Analyzer (CHNS-O EA1108—Italy). Results were corrected to Carbon (IAEA-CH6, EIL-72, and USGS-40) and Nitrogen standards (IAEA-N1 and IAEA-N2) (Fry et al., 1992).

2.3. Diatom Analysis

Diatom analysis was performed at an average sampling resolution of ca. 45 cal yr BP, at ~2.0 cm intervals, using 0.5 mL of sediment and standard methods (Battarbee, 1986; Bradbury, 1986). Known concentrations of residues were mounted using Naphrax® to determine diatom concentration. At least 300 diatom valves were identified per slide using an oil immersion DIC objective at 1000X magnification. See supporting information for authority names. Diatom concentration was calculated using known sediment concentrations. Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 1987) was performed using Tilia *v. 2.0.37* (Grimm, 2013). Taxa included in the cluster analysis occurred at least three times with an abundance greater than 2%. To determine the significant number of zones ($N = 4$), a broken stick model was used (Juggins, 2016).

2.4. Palynology and Charcoal Analysis

Pollen analysis has an average sampling resolution of ca. 22 cal yr BP, at 0.5–2.0 cm intervals. More detailed methods are in the supporting information and Fletcher et al. (2018). Percent fern taxa (*Blechnum* spp., *Dicksonia* spp., *Histiopteris* spp., Hymenophyllaceae, *Microsorum* spp., Phymatodes, and *Polystichum* spp.) were summed to represent lower canopy density. *Bauera rudioides* and Urticaceae pollen percentages were summed as an index for disturbance taxa. Cluster analysis (CONISS) was performed to identify pollen

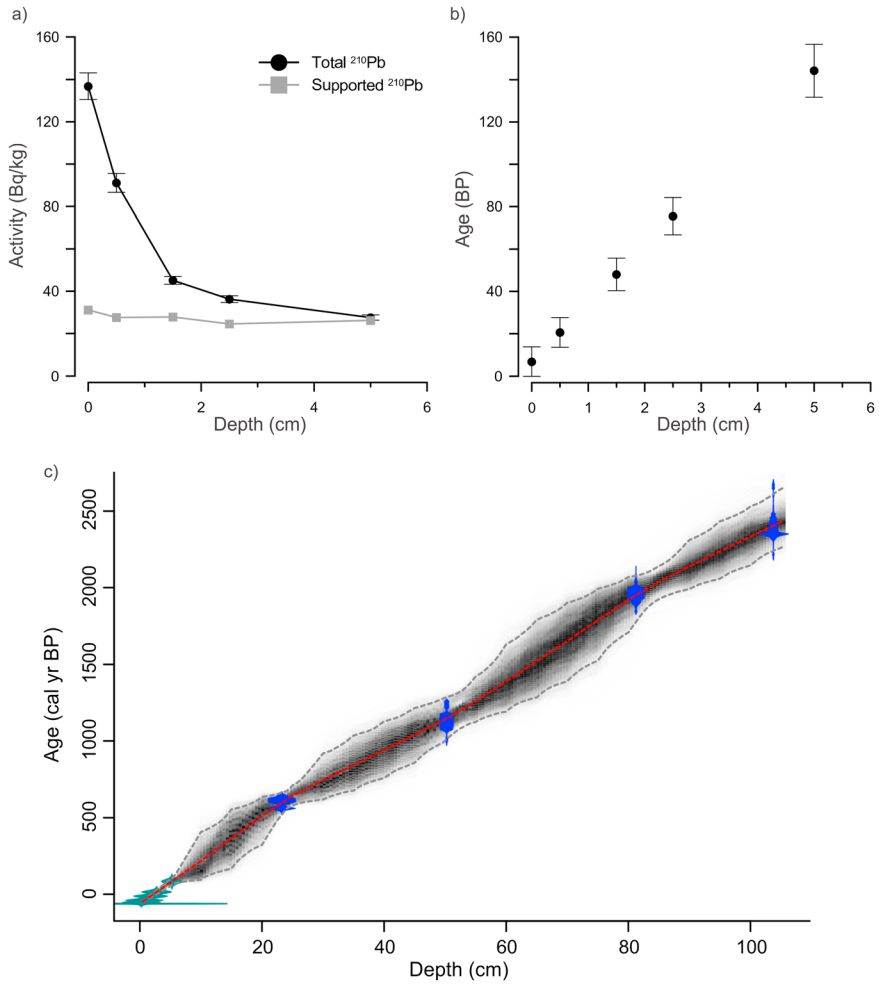

Figure 2. Age model for Lake Vera, Tasmania. (a) Total and supported ^{210}Pb activity concentrations with uncertainties, (b) ^{210}Pb chronology based on the CIC model, (c) Age model using Bacon, the blue symbols indicate probability distribution of the ^{14}C ages and the green symbols show the age probability of the ^{210}Pb dates. The black dotted lines demonstrate the 1,000 iterations of Bayesian statistic and potential depth ages in a 95% confidence interval (gray dotted line). The red dotted line demonstrates the age model chosen by weighted mean ages.

assemblage zones. Terrestrial taxa included in the cluster analysis occurred at least three times with an abundance greater than 2% to determine the significant number of zones (N = 4) using a broken stick model (supporting information).

Macroscopic charcoal was processed at 0.5 cm intervals, an average sampling resolution of ca. 12 cal yr BP, for the entire core length according to standard protocols (Whitlock & Larsen, 2001). A 1.5 cm^3 sample was soaked in household bleach then sieved (250 μm and 125 μm) for identification at 10–20X magnification. Microscopic charcoal was also enumerated during pollen identification. Charcoal particle size is a product of a range of factors including distance from fire, vegetation type, and fire intensity/severity (Mustaphi & Pisaric, 2014; Whitlock & Larsen, 2001). To understand broad changes in fire activity irrespective of charcoal particle size, we created a composite charcoal record by averaging the sum of microscopic and macroscopic charcoal data after converting each charcoal series to z-scores using the entire sequence (i.e., 2,400 years).

2.5. Numerical Analyses

2.5.1. Rate-of-Change

ROC analysis was run on proportional diatom and pollen data using the square chord distance measure standardized by the age intervals between samples to produce the ROC (Birks, 2012) in R *v. 3.4.1*. This ROC method does not require interpolation of data to even time steps, and we infer an increase in ROC as

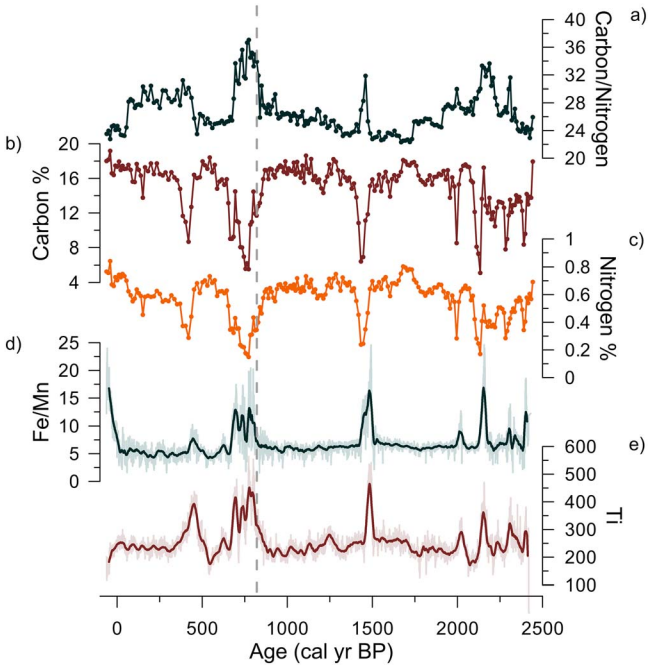

Figure 3. A summary of Lake Vera geochemical results of (a) Carbon/Nitrogen ratio, (b) Carbon percent, (c) Nitrogen percent, (d) Fe/Mn ratios fitted with a weighted average (window width = 51), and (e) Ti ratios fitted with a weighted average (window width = 51). Gray dashed line indicates the critical transition in the diatom community.

indicating a shift away from "equilibrium," and a concomitant increase in recovery time that signals a loss in resilience (Lim & Epureanu, 2011; Scheffer et al., 2009, 2012; Siteur et al., 2016). ROC was performed on taxa that occurred more than three times with a maximum abundance great than 2% for both Lake Vera diatoms and terrestrial pollen.

2.5.2. Principal Curves and Generalized Additive Models

A principal curve (PrC) was estimated on percentage diatom species and terrestrial pollen in *analogue v. 0.17–0* (Simpson & Oksanen, 2016) using R. PrCs are an alternative method to other ordination analyses for identifying the most important trend in the sediment sequence. A PrC is a nonlinear curve fitted through data in multiple dimensions that, unlike the linear methods used by Principal Component Analysis, can potentially represent greater explained variance if there is a single dominant gradient in the data (De' ath, G., 1999; Felde et al., 2014; Hastie & Stuetzle, 1989; Simpson & Birks, 2012). The PrC was initialized using the first correspondence analysis axis and subsequently estimated by fitting smoothing splines to abundances of individual taxa. The generalized cross-validation criterion was used to determine the wigglyness of each taxon's spline in the PrC. To avoid overfitting, a penalty on the degrees of freedom of 1.4 was applied. The diatom and terrestrial pollen taxa included in the PrC occurred more than three times with a maximum abundance over 2%.

Generalized additive models (GAMs) were fitted to the diatom and pollen PrCs to identify the important trends in the community data using mgcv *v. 1.8–15* (Wood, 2016) in R. GAMs are semiparametric models that use a sum of smooth functions to model nonlinear relationships between covariates and the response (Hastie & Tibshirani, 1990; Simpson & Anderson, 2009; Yee & Mitchell, 1991). Models were fitted using penalized residual maximum likelihood, in which a penalty controls the degree of wigglyness of the estimated trends (smooth functions) (Wood, 2011). Here we use a location-scale Gaussian GAM, which enables simultaneous estimation of both the mean and variance of a time series. See Bunting et al. (2016) for further details on the GAM modeling approach. We account for the implicit nonconstant variance that arises due to each sample representing a different amount of time by including this as a covariate in the linear predictor for the variance part of the model. This method is used to show the change in resilience of the lentic and terrestrial systems.

3. Results

3.1. Coring and Chronology

A summary of the radiocarbon results is presented in Table 1. The age model shows somewhat linear sedimentation with some variability throughout the sequence (Figure 2). Unsupported ^{210}Pb activity reached background at 5 cm. The Bayesian age model determined a mean accumulation rate of 20 yr/cm (Figure 2). For more details on ^{210}Pb results see supporting information.

3.2. Geochemical Analysis

The Fe/Mn ratio demonstrates dynamic variability in this record; increasing values occur at ca. 2,200 cal yr BP, from ca. 1,550 to 1,400 and ca. 800 to 600 cal yr BP. Rising values occur from ca. 0 cal yr BP to present and are likely the result of XRF sampling near the core end (Figure 3d). Ti shows similar trends as Fe/Mn with an opposing decreasing trend from 0 cal yr BP to present (Figure 3e). A further summary of the XRF geochemical results can be found in the supporting information.

Carbon and Nitrogen percentages show similar trends, while C/N has opposing trends (Figure 3). C/N (C% and N%) increases (decreases) from ca. 2,400 to 2,100 cal yr BP, followed by a decline (incline) to ca. 1,400 cal yr BP where a sharp peak (trough) occurs. Low (high) stable values occur until 880 cal yr BP where C/N (C% and N%) increases (decreases) rapidly from ca. 880 to 720 cal yr BP, low (high) stable values resume when C/N (C% and N%) rapidly increases (decreases) ca. 550 cal yr BP and slowly declines (inclines) until present (Figure 3).

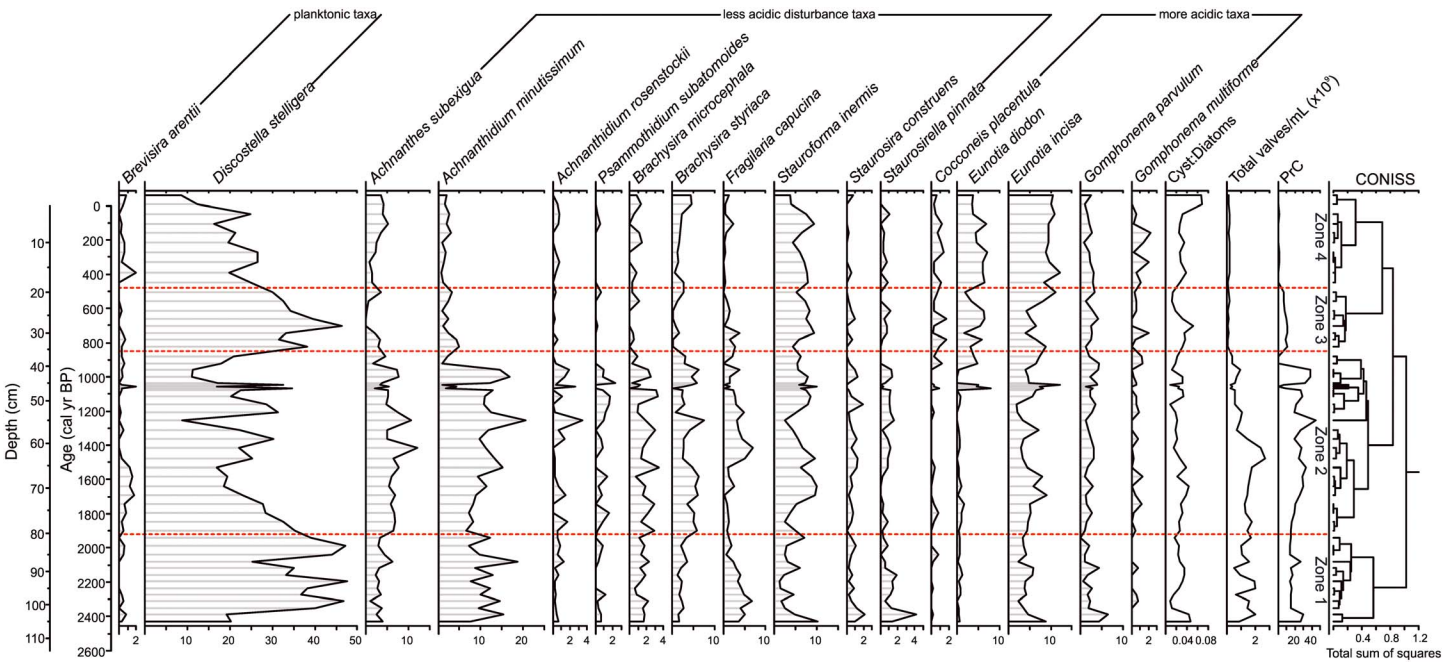

Figure 4. Stratigraphy of the important Lake Vera diatom species presented as percentage composition. The PrC estimates trends in the diatom percentage data (PrC explained variance = 60.0%). Red dashed lines show breaks in CONISS cluster analysis for diatom taxa above 2% abundance and that occur at least three times (four significant zones). *X* axis scale varies by taxa.

3.3. Diatom Analysis

Diatoms show good preservation throughout this record with 255 taxa identified from 57 depth samples. Four significant CONISS zones were identified in this record: Zone 1–2,427 to 1,939 cal yr BP, Zone 2–1,901 to 880 cal yr BP, Zone 3–820 to 506 cal yr BP, and Zone 4–448 cal yr BP to present (Figure 4).

Discostella stelligera dominates throughout the sediment record (>20%). In Zone 1 dominant taxa include the following: *Discostella stelligera* (30–40%), *Achnanthidium minutissimum* (~15%), *Stauroforma inermis* (~5%), *Eunotia incisa* (~5%), *Achnanthes subexigua* (~4%), *Fragilaria capucina* (~4%), and *Gomphonema parvulum* (~3%) with high stability through this zone. Within this zone the total diatom valves are high, averaging around 1.6×10^8 valves/mL yr^{-1}. Zone 2 taxa are similar to Zone 1 with the exception of an increase in *Brachysira styriaca* (~4%) and *A. subexigua* (~5–10%), while *Discostella stelligera* (~20%) declines in abundance. In this zone, the total valves remain high, peaking at ca. 1,480 cal yr BP, before declining to the end of the zone.

Zone 3 begins at ca. 820 cal yr BP with a sharp decline in *A. minutissimum* (~2%), *A. subexigua* (~1–5%), and *B. styriaca* (~2%); and increased abundance of *D. stelligera* (40–50%), *Eunotia diodon* (5%), *Frustulia elongatissima* (8–10%), and *Gomphonema multiforme* (4%). Total valves are very low throughout this zone and the next. Zone 4 has a decrease in *D. stelligera* (~20%) and a slight increase in *A. subexigua* (~5%), *Brevisira arentii* (~1–2%), *B. styriaca* (~4%), and *E. incisa* (~10%).

3.4. Palynology and Charcoal Analysis

We observe four significant CONISS zones from the percent terrestrial pollen taxa: Zone 4—2,429 to 2,098 cal yr BP; Zone 3—2,078 to 802 cal yr BP; Zone 2—783 cal yr BP to 562 cal yr BP; and Zone 1—536 cal yr BP to present (supporting information). *Pediastrum* spp. influx has low values from 2,440 to 1,250 cal yr BP followed by an increase to peak at 900 cal yr BP. *Pediastrum* spp. sharply declines with a slight increase and variable influx to present (Figure 5d). Total percent ferns remain low from ca. 2,430 cal yr BP to ca. 760 cal yr BP followed by a sharp increase and high variability. Ferns remain high for the remainder of the record with a decreasing trend (Figure 5b). Percent disturbance taxa (Urticaceae and *Bauera rudioides*) gradually increase from 2,430 to 880 cal yr BP followed by a decline to ca. 745 cal yr BP. Disturbance taxa then increase in abundance and variability for the remainder of the record (Figure 5a). A pollen stratigraphy summarizing the major

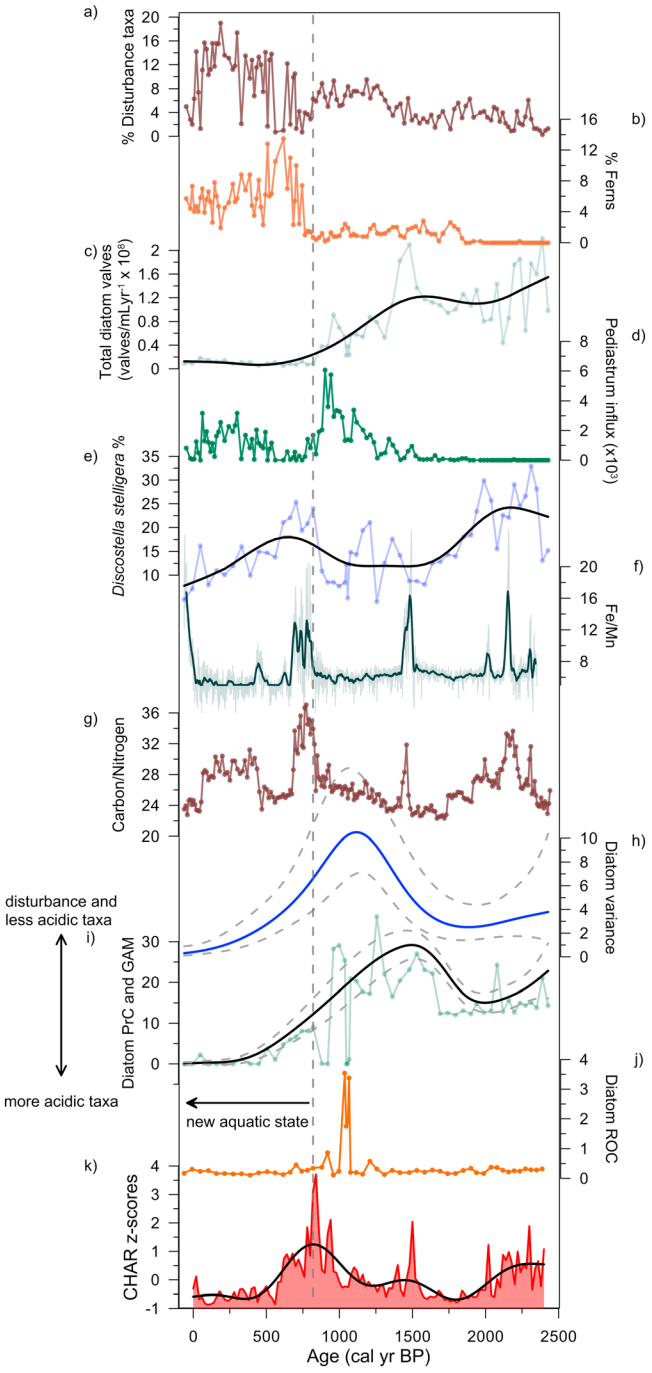

Figure 5. A summary plot of Lake Vera data. (a) Percent disturbance pollen taxa (Urticaceae and *Bauera rubioides*) (brown), (b) total percent fern pollen taxa (orange), (c) total diatoms valves (valves/mL $\times 10^8$) (light green) fitted with a generalized additive model (GAM) (black), (d) *Pediastrum* influx ($\times 10^3$) (green), (e) *Discostella stelligera* percentages (blue) with a fitted GAM (black), (f) Fe/Mn ratios (gray) fitted with a weighted average in dark green (window width = 33), (g) Carbon/Nitrogen ratio (brown), (h) diatom variance (blue) and confidence interval (gray dashed) of GAM residuals, (i) diatom PrC (green) with fitted GAM (black) and confidence intervals (gray dashed), (j) diatom ROC (orange), and (k) Charcoal sum z-scores (red) with a fitted GAM (black). Gray dotted line indicates the timing of the diatom critical transition.

taxa and compositional transitions is included in the supporting information. The charcoal sum z-scores show three time periods of increased charcoal from ca. 2,400 to 2,000 cal yr BP, at ca. 1,500 cal yr BP and from ca. 940 to 660 cal yr BP (Figure 5k).

3.5. Numerical Analyses

3.5.1. Rate-of-Change

Diatom ROC is very low (below 0.5) until ca. 1,070 cal yr BP where peak values (3.5) occur until ca. 1,040 cal yr BP. Values decline again to below 0.5 for the remainder of the record (Figure 6a). The pollen ROC remains below 0.5 until ca. 780 cal yr BP then increases to 2.9 and becomes highly variable until present (Figure 6e).

3.5.2. Principal Curves and Generalized Additive Models

The PrC has an explained variance of 60.0% for diatoms and 60.7% for the terrestrial pollen. Low values of the diatom PrC are associated with more acidic taxa and high values with less acidic disturbance taxa. The diatom PrC is fairly stable with a slight declining trend from ca. 2,430 to 1,900 cal yr BP followed by a rapid increase with high variability until ca. 880 cal yr BP. From ca. 820 cal yr BP to present, the diatom PrC gently decline with low very stable values (Figure 6c). The pollen PrC, however, demonstrates a decreasing trend throughout the record, with abrupt high variability from ca. 750 cal yr BP to present (Figure 6g). Low pollen PrC values are associated with disturbance taxa, middle values with wet rain forest taxa and high values with low canopy cover taxa (Ericaceae, *Pomaderris* spp., Proteaceae, Poaceae). Species abundance gradients for both the diatoms and terrestrial pollen PrC are included in the supporting information.

The diatom fitted GAM declines from ca. 2,430 to 1,940 cal yr BP and increases to peak at ca. 1,450 cal yr BP then declines to low stable values from ca. 500 cal yr BP to present (Figure 6c). The variance of the diatom GAM residuals show a slight decline from ca. 2,430 to 1,780 cal yr BP followed by an increasing trend peaking at ca.1,070 cal yr BP and declining to low values from ca. 500 cal yr BP to present (Figure 6b). The pollen GAM demonstrates a linear decreasing model through the PrC (Figure 6g). The variance of the pollen GAM increases and plateaus between ca. 1,850 and 1,450 cal yr BP, followed by a decline. The pollen variance starts to rapidly increase at ca. 820 cal yr BP, peaking at ca. 490 cal yr BP followed by a small decline. The variance increases slightly from ca. 60 cal yr BP to present (Figure 6f).

4. Discussion

4.1. Fire-Driven Changes in Aquatic Ecosystem Dynamics

The pivotal role of fire in the terrestrial ecology of western Tasmania is well understood (Bowman et al., 2009; Fletcher et al., 2014; Jackson, 1968), yet little is known about how fire-driven vegetation change influences aquatic ecosystems within this landscape. The deep organic soils that form under rain forest vegetation in this region are highly combustible when dry (di Folco & Kirkpatrick, 2013; Pemberton, 1988, 1989). Indeed, fires within the rain forest only occur under anomalously dry conditions (Styger & Kirkpatrick, 2015), and the substantial available biomass in these systems often results in high-intensity forest fires that can completely incinerate the underlying organic soil profiles. Subsequent rainfall events can strip the soil profile from the landscape (Bowman & Jackson, 1981; di

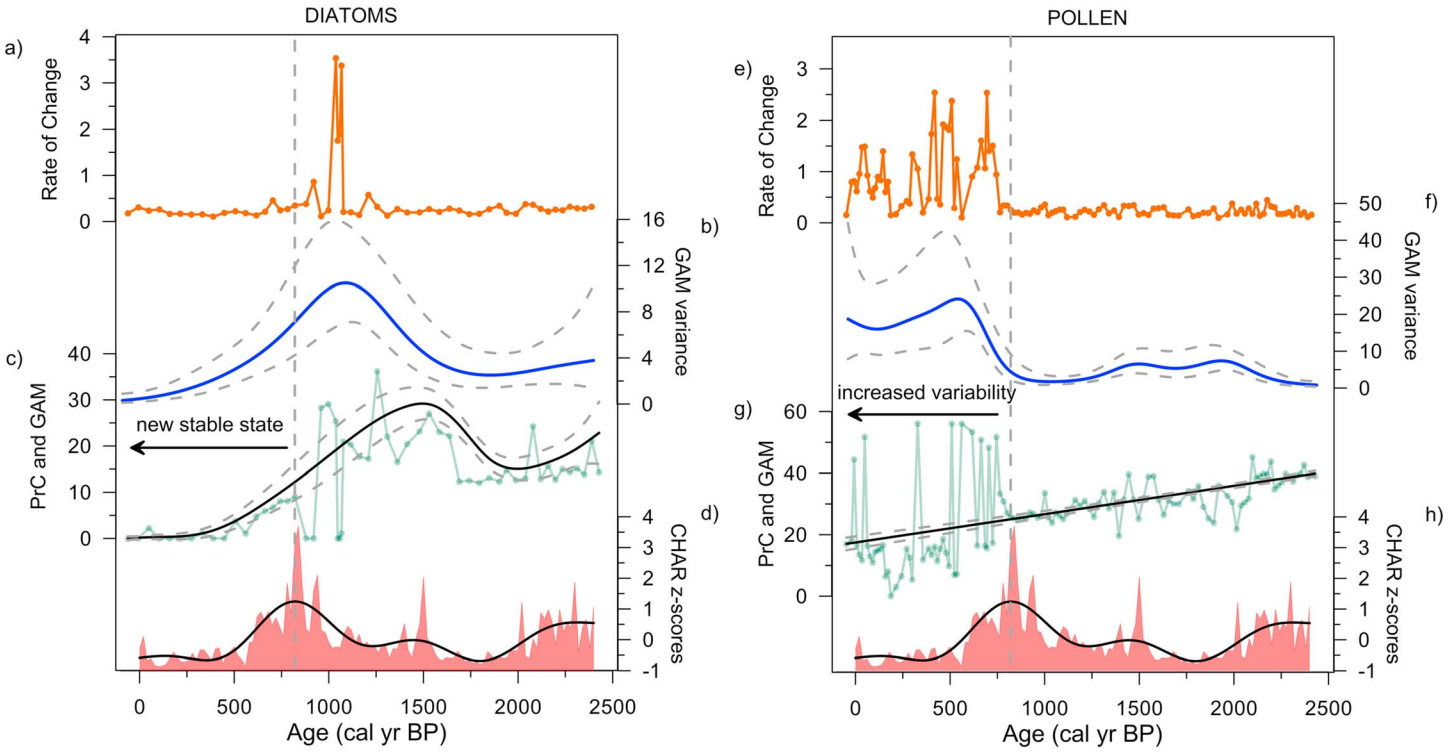

Figure 6. Critical transition statistical summary of the Lake Vera diatoms (left) and pollen (right) including: (a and e) ROC (orange), (b and f) GAM fitted variance (blue) and confidence intervals (gray dashed line); (c and g) PrC (green), fitted GAM (black), and confidence intervals (gray dashed); (d and h) Charcoal (CHAR in red) sum z-scores and fitted GAM (black). Vertical gray dashed lines indicate the timing of the diatom critical transition.

Folco & Kirkpatrick, 2013; Jackson, 1968; Pemberton, 1988, 1989), depositing large amounts of terrestrially derived material into aquatic systems (Townsend & Douglas, 2000). Increased input of terrestrial material into lakes can result in less light penetration, less oxic conditions resulting from less mixing, and anoxic lake bottom waters (Augustinus et al., 2012; Carignan & Tessier, 1988; Cohen, 2003; Koinig et al., 2003). Further, burning of the catchment organic soil profile causes a release of organically bound Fe into watersheds increasing preserved Fe in sediments (Ketterings et al., 2000; Korhola et al., 1996).

While a series of fire events within the rain forest-dominant Lake Vera catchment (ca. 2,200, 1,500 and 800 cal yr BP) initially fail to provoke a shift in the pollen record (Figures 5a, 5b, 6e, and 6g), these fire events are associated with an influx of terrestrially derived carbon (Figure 5g), increases in the importance of the diatom *Discostella stelligera* (Figure 5e) and changes in other sediment geochemical properties (such as an increase in Ti and Fe/Mn; Figures 3e and 5f). *Discostella stelligera* (Figure 5e) is a planktonic diatom taxon with broad ecological tolerances that is favored by relatively shallow mixing depths and increased nutrient availability (Korhola et al., 1996; Saros et al., 2012; Saros & Anderson, 2015). We, thus, interpret our data as reflecting a lowering of lake mixing depth resulting from an increase in turbidity and less light availability following fire-driven influxes of organic matter and Fe into Lake Vera (Fee et al., 1996; Korhola et al., 1996). Further, elevated diatom productivity and high relative importance of disturbance diatom taxa, *Achnanthidium minutissimum* and *Fragilaria capucina*, from ca. 2,430 to 880 cal yr BP (Figures 4 and 5i) are consistent with the effects of fire-related increases in terrestrial organic matter inputs into the lake (Hodgson et al., 1996; Saunders et al., 2013). Damage to terrestrial vegetation by fire can destabilize soil profiles, resulting in erosion of terrestrial organic material (C/N; Figure 5g) and inorganic (Ti; Figure 3e) material into lakes that favors disturbance diatom taxa (higher PrC values; Figures 5i). Additionally, increased ash deposition can increase the base cation content buffering lake pH, also favoring these less acidic diatom taxa (Haberle et al., 2006; Korhola et al., 1996).

A sudden diatom compositional shift occurs at ca. 880 cal yr BP (Figure 4): from a less acidophilous community (i.e., *Achnanthidium minutissimum*, *Achnanthes subexigua*, *Achnanthidium rosenstockii*, *Psammothidium subatomoides*, *Brachysira styriaca*, *B. microcephala*, *Fragilaria capucina*, *Staurosira construens*, and

Staurosirella pinnata) to a more acidophilous community (i.e., *Brevisira arentii*, *Eunotia diodon*, *Eunotia incisa*, *Eunotia* spp., *Frustulia elongatissima*, *Gomphonema multiforme*, and *Cocconeis placentula*) (Bradbury, 1986; Hodgson et al., 2000; Vyverman et al., 1996). This diatom shift is preceded by a decline in diatom productivity (Figure 5c), low charcoal deposition (low fire activity; Figure 5k), decreased terrestrial carbon input into the lake (Figure 5g), and an increase in *Pediastrum* (at ca. 1,420 cal yr BP; Figure 5d), a freshwater algae found in the littoral zones of clear oligotrophic acidic lakes (Weckström et al., 2010). These trends suggest a prolonged low fire period (between ca. 1,460 to 960 cal yr BP) and an associated reduction in terrestrial material inputs (organic soil products and ash) into Lake Vera that led to clearer and more oligotrophic waters, lower diatom productivity, and increased acidification of the lake (Figure 5i).

The remainder of the sequence is characterized by the absence of disturbance taxa (*A. minutissimum* and *F. capucina*) and a persistence of an oligotrophic/acidophilus diatom community (*E. diodon*, *E. incisa*, *F. elongatissima*, and *G. multiforme*; Figure 4). While a fire event at ca. 940 cal yr BP drove an increase in terrestrially derived carbon, Fe/Mn and *D. stelligera*, the diatom community appears complacent throughout the remainder of the sequence (Figure 5). The apparent permanence of this shift through the remaining ~820 years, despite marked variability in catchment fire activity and the input of terrestrially derived material into the lake, reveals a remarkably stable diatom community through this time (Figure 6).

4.2. Critical Transitions and Early Warning Signals

4.2.1. The Aquatic System

We observe a nonlinear diatom community state shift (i.e., critical transition) at ca. 820 cal yr BP that we interpret as a response to the cumulative effect of fire-driven perturbations within the local catchment (Figures 5 and 6). This shift affords us the opportunity to test for the presence of EWS of this critical transition in our data. Given the potential problems associated with data manipulation (i.e., interpolation), we focus on two measurements of ecosystem resilience considered robust for palaeoecological data: variance and ROC (Lim & Epureanu, 2011; Scheffer et al., 2012; Siteur et al., 2016). Ecological theory on critical transitions predicts that increased variance occurs as a system approaches a critical transition (Scheffer et al., 2009, 2012). While ROC is a measure of how rapidly a system state deviates from a stable steady state in response to a perturbation or a change in external conditions. With critical transitions, ROC increases when a system is unable to cope with the rapid changes (i.e., above some critical ROC threshold) and recovery slows (Dakos et al., 2012; Lim & Epureanu, 2011; Scheffer et al., 2009, 2012; Siteur et al., 2016).

At Lake Vera, fire-driven changes in the delivery of terrestrially derived organic and inorganic sediment into the lake had a profound influence on lake conditions and diatom community structure through the last ~2,400 years. These are manifest as shifts in lake water trophic status, pH, turbidity, and mixing conditions that drove clear changes in diatom community dynamics. Importantly, we observe a clear increase in ecosystem variance between ca. 1,780 to 1,070 cal yr BP in response to this suite of changes and prior to the critical transition in the diatom community (Figures 5h and 6b). Further, we observe a marked decrease in variance of the new diatom community state, suggesting a shift to a more resilient stable state, consistent with ecological theory, indicating that variance is a valid and measurable EWS in this system (Carpenter & Brock, 2006; Dakos et al., 2012, 2015; Scheffer et al., 2009, 2012).

Further, we observe a marked increase in the ROC in the diatom community between ca. 1,070 to 1,040 cal yr BP (Figures 5j and 6a), reflecting rapid shifts in the system state away from equilibrium as it becomes unstable close to a bifurcation point. The shift to low ROC values following the critical transition suggests a shift to a new stable diatom community state, consistent with the reduction in variance following this critical transition. These results suggest that variance and ROC are useful EWS metrics for detecting critical transitions in this aquatic system and that monitoring programs designed to detect potential critical transitions might benefit from measuring these variables. We conclude that the resilience of the diatom community was likely eroded by the cumulative influence of fire-driven catchment disturbance (principally via terrestrial organic matter inputs) over lake water trophic status, pH, turbidity, and mixing conditions. While the diatom community state shift occurs in concert with a fire-driven influx of terrestrial organic matter, the fact that both variance and ROC increase through a phase of low catchment fire activity and low terrestrial matter influx (ca. 1,400 to 900 cal yr BP) implies that the loss of resilience of this system occurred in response to the cumulative effect of repeated fire-driven changes within the catchment, rather than in response to a discrete event.

4.2.2. The Terrestrial System

Despite marked changes in the Lake Vera aquatic ecosystem driven by burning of the local catchment, the pollen from Lake Vera shows a degree of complacency to fire (Figures 6e–6h). Indeed, the pollen PrC values remain remarkably stable between 2,430 to 800 cal yr BP, despite clear fire-driven disturbance of the local catchment (Figure 5). This complacency to fire of the local rain forest system stand contrasts the hypersensitivity displayed by rain forest to fire in this landscape (Beck et al., 2017; Bowman & Jackson, 1981; Fletcher et al., 2014; Kirkpatrick & Hardwood, 1980). It is important to note that the source area of airborne pollen into a lake is often considerably larger than the local lake catchment (Bunting et al., 2004; Prentice, 1978; Sugita, 1993). Consequently, the apparent complacency of the vegetation system to fire might reflect the discrepancy between the size of burnt catchment area relative to the pollen source area (i.e., an insensitivity of pollen data to the scale of fire events and associated vegetation change, Figures 5a, 5b, and 6g).

Importantly, we do observe a marked shift in variance and ROC of the pollen assemblage following the fire event that occurred from ca. 940 to 660 cal yr BP (Figures 6e–6h), suggesting lost resilience within the local rain forest. The fire event at ca. 840 cal yr BP is associated with an increase in forest taxa that thrive with disturbance (Urticaceae and *Baeura rubioides*; Figure 5a) (Fletcher et al., 2018), ground ferns favored by increased light penetration through a forest canopy (e.g., *Blechnum* spp.; Figure 5b) (Saldaña et al., 2010) and a sustained increase in *Eucalyptus*, a plant with highly flammable foliage that can alter local fire regimes and effectively remove fire-sensitive rain forest vegetation (Bowman, 1998, 2000; Fletcher et al., 2014; Fletcher, Wood, & Haberle, 2014; Wood & Bowman, 2012). We interpret this suite of changes in the terrestrial system as reflecting the cumulative effect of repeated fires on the resilience of this rain forest system via an opening of the canopy and an invasion by fire-promoting species, thus increasing the probability of future burning and localized rain forest extinction (sensu; Fletcher et al., 2014; Fletcher, Wood, & Haberle, 2014). Our evidence for an increase in both variance and ROC of the vegetation surrounding Lake Vera demonstrates the efficacy of these metrics as potential EWS of the rain forest system around Lake Vera and, importantly, implies that these EWS metrics might be relevant and measurable indicators across a range of natural systems.

5. Conclusion

The diatom community demonstrates a nonlinear shift from less oligotrophic acidic taxa to more oligotrophic acidic taxa at ca. 820 cal yr BP due to the cumulative effects of fire-driven changes in the amount and type of terrestrial material deposited into the lake system. This critical transition is preceded by clear and measurable EWS: increased system state variability and ROC. The new diatom state displays less variability and a complacency to continued catchment disturbance by fire, suggesting a shift to a more resilient stable state. The terrestrial vegetation, on the other hand, appears complacent to repeated burning through the early part of the record, with a marked increase in variability and ROC following the diatom state shift suggesting that this system is approaching a critical transition. We conclude that (1) the diatom community is highly sensitive to fire-driven terrestrial ecosystem change; (2) that system state variance and ROC are useful EWS of nonlinear aquatic and terrestrial ecosystem change; and (3) these metrics have the potential as EWS across a range of natural systems.

Acknowledgments

The financial support of this project comes from the Australian Research Council (award: DI110100019 and IN140100050) and Australian Institute of Nuclear Science and Engineering (award: ALNGRA12003P).

Gavin L. Simpson was supported by the Natural Sciences and Engineering Research Council of Canada's Discovery Grant Program. We would like to thank Tasmania National Parks and Wildlife Service and the Tasmanian Aboriginal Community for their support and allowing us to work on their lands. We would also like to thank Michela Mariani, Anthony Romano, Coralie Tate, and Valentina Vanghi for their assistance in the field. We would like to acknowledge Brent Wolfe and his laboratory at University of Waterloo, Waterloo, Canada (adjunct with Wilfrid Laurier University, Waterloo, Canada) for their isotopic analysis and interpretation assistance. The data presented are listed in the tables, references, and supplements, as well as, publicly available on Neotoma (https://www.neotomadb.org/) upon date of publication. We also thank two anonymous referees for their helpful comments on a previous draft.

References

Appleby, P., & Oldfield, F. (1978). The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. *Catena*, *5*(1), 1–8. https://doi.org/10.1016/S0341-8162(78)80002-2

Aquatic Research Instruments (2016). *Universal Percussion Corer*, edited. Indiana: Aquatic Research Instruments.

Atahan, P., Heijnis, H., Dodson, J., Grice, K., Le Métayer, P., Taffs, K., et al. (2015). Pollen, biomarker and stable isotope evidence of late Quaternary environmental change at Lake McKenzie, southeast Queensland. *Journal of Paleolimnology*, *53*(1), 139–156. https://doi.org/10.1007/s10933-014-9813-3

Augustinus, P., Cochran, U., Kattel, G., & D'Costa, D. (2012). Late Quaternary paleolimnology of Onepoto maar, Auckland, New Zealand: Implications for the drivers of regional paleoclimate. *Quaternary International*, *253*, 18–31. https://doi.org/10.1016/j.quaint.2011.02.028

Battarbee, R. W. (1986). Diatom analysis. In B. E. Berglund (Ed.), *Handbook palaeoecology and palaeohydrology* (pp. 527–570). Chichester: John Wiley.

Beck, K. K., Fletcher, M.-S., Gadd, P. S., Heijnis, H., & Jacobsen, G. E. (2017). An early onset of ENSO influence in the extra-tropics of the southwest Pacific inferred from a 14, 600 year high resolution multi-proxy record from Paddy's Lake, northwest Tasmania. *Quaternary Science Reviews*, *157*, 164–175. https://doi.org/10.1016/j.quascirev.2016.12.001

Birks, H. J. B. (2012). Overview of numerical methods in palaeolimnology. In H. J. B. Birks, et al. (Eds.), *Tracking environmental change using lake sediments: Data handling and numerical techniques* (pp. 19–92). Netherlands: Springer. https://doi.org/10.1007/978-94-007-2745-8_2

Blaauw, M., & Christen, J. A. (2013). Bacon manual- v2.2 (Rep.) (pp. 1–11).

Bowman, D. (1998). The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist*, *140*(3), 385–410. https://doi.org/10.1111/j.1469-8137.1998.00289.x

Bowman, D. (2000). *Australian rainforests: Islands of green in a land of fire*. Cambridge UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511583490

Bowman, D., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., et al. (2009). Fire in the Earth system. *Science*, *324*(5926), 481–484. https://doi.org/10.1126/science.1163886

Bowman, D., & Jackson, W. (1981). Vegetation succession in southwest Tasmania. *Search*, *12*(10), 358–362.

Bradbury, P. J. (1986). Late Pleistocene and Holocene paleolimnology of two mountain lakes in western Tasmania. *PALAIOS*, *1*(4), 381–388. https://doi.org/10.2307/3514475

Bunting, L., Leavitt, P. R., Simpson, G. L., Wissel, B., Laird, K. R., Cumming, B. F., et al. (2016). Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. *Limnology and Oceanography*, *61*(6), 2090–2107. https://doi.org/10.1002/lno.10355

Bunting, M. J., Gaillard, M. J., Sugita, S., Middleton, R., & Broström, A. (2004). Vegetation structure and pollen source area. *The Holocene*, *14*(5), 651–660. https://doi.org/10.1191/0959683604hl744rp

Carignan, R., & Tessier, A. (1988). The co-diagenesis of sulfur and iron in acid lake sediments of southwestern Quebec. *Geochimica et Cosmochimica Acta*, *52*(5), 1179–1188. https://doi.org/10.1016/0016-7037(88)90271-2

Carpenter, S. R., & Brock, W. A. (2006). Rising variance: A leading indicator of ecological transition. *Ecology Letters*, *9*(3), 311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x

Carstensen, J., Telford, R. J., & Birks, J. H. B. (2013). Diatom flickering prior to regime shift. *Nature*, *498*(7455), E11–E12. https://doi.org/10.1038/nature12272

Cohen, A. S. (2003). *Paleolimnology: The history and evolution of lake systems* (525 pp.). USA: Oxford University Press.

Croudace, I. W., & Rothwell, R. G. (2015). *Micro-XRF studies of sediment cores: Applications of a non-destructive tool for the environmental sciences*. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9849-5

Dakos, V., Carpenter, S. R., Brock, W. A., Ellison, A. M., Guttal, V., Ives, A. R., et al. (2012). Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS One*, *7*(7), e41010. https://doi.org/10.1371/journal.pone.0041010

Dakos, V., Carpenter, S. R., van Nes, E. H., & Scheffer, M. (2015). Resilience indicators: Prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *370*(1659), 20130263. https://doi.org/10.1098/rstb.2013.0263

De' ath, G. (1999). Principal curves: A new technique for indirect and direct gradient analysis. *Ecology*, *80*(7), 2237–2253. https://doi.org/10.1890/0012-9658(1999)080%5B2237:PCANTF%5D2.0.CO;2

Department of Primary Industries, P., Water and Environment (Tasmania) (2017). *TASVEG—The digital vegetation map of Tasmania*, Edited. Tasmania: Tasmanian Government.

di Folco, M. B., & Kirkpatrick, J. B. (2013). Organic soils provide evidence of spatial variation in human-induced vegetation change following European occupation of Tasmania. *Journal of Biogeography*, *40*(1), 197–205. https://doi.org/10.1111/j.1365-2699.2012.02779.x

Fee, E. J., Hecky, R. E., Kasian, S. E. M., & Cruikshank, D. R. (1996). Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnology and Oceanography*, *41*(5), 912–920. https://doi.org/10.4319/lo.1996.41.5.0912

Felde, V. A., Bjune, A. E., Grytnes, J. A., & Birks, H. J. B. (2014). A comparison of novel and traditional numerical methods for the analysis of modern pollen assemblages from major vegetation–landform types. *Review of Palaeobotany and Palynology*, *210*, 22–36. https://doi.org/10.1016/j.revpalbo.2014.06.003

Fletcher, M.-S., Benson, A., Bowman, D. M. J. S., Gadd, P. S., Heijnis, H., Mariani, M., et al. (2018). Centennial-scale trends in the Southern Annular Mode revealed by hemisphere-wide fire and hydroclimatic trends over the last 2400 years. *Geology*. https://doi.org/10.1130/G39661.1

Fletcher, M. S., & Thomas, I. (2010). The origin and temporal development of an ancient cultural landscape. *Journal of Biogeography*, *37*(11), 2183–2196. https://doi.org/10.1111/j.1365-2699.2010.02363.x

Fletcher, M.-S., Wolfe, B. B., Whitlock, C., Pompeani, D. P., Heijnis, H., Haberle, S. G., et al. (2014). The legacy of mid-Holocene fire on a Tasmanian montane landscape. *Journal of Biogeography*, *41*(3), 476–488. https://doi.org/10.1111/jbi.12229

Fletcher, M.-S., Wood, S. W., & Haberle, S. G. (2014). A fire-driven shift from forest to non-forest: Evidence for alternative stable states? *Ecology*, *95*(9), 2504–2513. https://doi.org/10.1890/12-1766.1

Fry, B., Brand, W., & Mersch, F. J. (1992). Automated analysis system for coupled δ13C and δ15N measurements. *Analytical Chemistry*, *64*(3), 288–291. https://doi.org/10.1021/ac00027a009

Gentilli, J. (1971). *Climates of Australia and New Zealand* (405 pp.). Amsterdam: Elsevier Science Ltd.

Gillett, N. P., Kell, T. D., & Jones, P. D. (2006). Regional climate impacts of the Southern Annular Mode. *Geophysical Research Letters*, *33*, L23704. https://doi.org/10.1029/2006GL027721

Grimm, E. C. (1987). CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, *13*(1), 13–35. https://doi.org/10.1016/0098-3004(87)90022-7

Grimm, E. C. (2013). *Tilia*, Edited. IL: Illinois State Museum Research and Collection Centre.

Haberle, S. G., Tibby, J., Dimitriadis, S., & Heijnis, H. (2006). The impact of European occupation on terrestrial and aquatic ecosystem dynamics in an Australian tropical rain forest. *Journal of Ecology*, *94*(5), 987–1002. https://doi.org/10.1111/j.1365-2745.2006.01140.x

Hastie, T., & Stuetzle, W. (1989). Principal curves. *Journal of the American Statistical Association*, *84*(406), 502–516. https://doi.org/10.2307/2289936

Hastie, T., & Tibshirani, R. (1990). *Generalized additive models*. CRC Press. https://doi.org/10.1002/0471667196.ess0297.pub2

Hill, K. J., Santoso, A., & England, M. H. (2009). Interannual Tasmanian rainfall variability associated with large-scale climate modes. *Journal of Climate*, *22*(16), 4383–4397. https://doi.org/10.1175/2009JCLI2769.1

Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, *30*(9), 503–506. https://doi.org/10.1016/j.tree.2015.06.010

Hodgson, D., Tyler, P., & Vyverman, W. (1996). The palaeolimnology of Lake Fidler, a meromictic lake in south-west Tasmania and the significance of recent human impact. *Journal of Paleolimnology*, *18*(4), 313–333. https://doi.org/10.1023/A:1007995614287

Hodgson, D. A., Vyverman, W., Chepstow-Lusty, A., & Tyler, P. A. (2000). From rainforest to wasteland in 100 years: The limnological legacy of the Queenstown mines, Western Tasmania. *Archiv für Hydrobiologie*, *146*(1), 153–176.

Hogg, A., Hua, Q., Blackwell, P., Niu, M., Buck, C., Guilderson, T., & Zimmerman, S. (2013). SHCal13 Southern Hemisphere Calibration, 0–50,000 years cal BP. *Radiocarbon*, *55*(04), 1889–1903. https://doi.org/10.2458/azu_js_rc.55.16783

Isbell, R. F. (2002). *The Australian soil classification: Revised edition*. Collingwood, VIC, Australia: CSIRO.

Jackson, W. (1968). *Fire, air, water and Earth—An elemental ecology of Tasmania*. Paper Presented at Proceedings of the Ecological Society of Australia, Canberra, Australia.

Juggins, S. (2016). Package 'rioja'. In *Analysis of Quaternary Science Data*, Edited.

Ketterings, Q. M., Bigham, J. M., & Laperche, V. (2000). Changes in soil mineralogy and texture caused by slash-and-burn fires in Sumatra, Indonesia. *Soil Science Society of America Journal*, *64*(3), 1108–1117. https://doi.org/10.2136/sssaj2000.6431108x

Kirkpatrick, J., & Hardwood, C. E. (1980). Vegetation of an infrequently burned Tasmanian mountain region. *Proceedings of the Royal Society of Victoria*, *91*, 79–102.

Kitchener, A., & Harris, S. (2013). *From forest to fjaeldmark: Description of Tasmania's vegetation* (2nd ed.). Tasmania: Department of Primary Industries, Parks, Water and Environment.

Koinig, K. A., Shotyk, W., Lotter, A. F., Ohlendorf, C., & Sturm, M. (2003). 9000 years of geochemical evolution of lithogenic major and trace elements in the sediment of an alpine lake—The role of climate, vegetation, and land-use history. *Journal of Paleolimnology*, *30*(3), 307–320. https://doi.org/10.1023/A:1026080712312

Korhola, A., Virkanen, J., Tikkanen, M., & Blom, T. (1996). Fire-induced pH rise in a naturally acid hill-top lake, southern Finland: A palaeoecological survey. *Journal of Ecology*, *84*(2), 257–265. https://doi.org/10.2307/2261361

Kylander, M. E., Ampel, L., Wohlfarth, B., & Veres, D. (2011). High-resolution X-ray fluorescence core scanning analysis of Les Echets (France) sedimentary sequence: New insights from chemical proxies. *Journal of Quaternary Science*, *26*(1), 109–117. https://doi.org/10.1002/jqs.1438

Lenton, T. M. (2011). Early warning of climate tipping points. *Nature Climate Change*, *1*(4), 201–209. https://doi.org/10.1038/nclimate1143

Lim, J., & Epureanu, B. I. (2011). Forecasting a class of bifurcations: Theory and experiment. *Physical Review E*, *83*(1), 016203. https://doi.org/10.1103/PhysRevE.83.016203

Macphail, M. K. (1979). Vegetation and climates in southern Tasmania since the last glaciation. *Quaternary Research*, *11*(03), 306–341. https://doi.org/10.1016/0033-5894(79)90078-4

Mariani, M., & Fletcher, M. S. (2016). The Southern Annular Mode determines inter-annual and centennial-scale fire activity in temperate southwest Tasmania, Australia. *Geophysical Research Letters*, *43*, 1702–1709. https://doi.org/10.1002/2016GL068082

Markgraf, V., Bradbury, P. J., & Busby, J. R. (1986). Paleoclimates in southwestern Tasmania during the last 13,000 years. *PALAIOS*, *1*(4), 368–380. https://doi.org/10.2307/3514474

Mustaphi, C. J. C., & Pisaric, M. F. J. (2014). A classification for macroscopic charcoal morphologies found in Holocene lacustrine sediments. *Progress in Physical Geography*, *38*(6), 734–754. https://doi.org/10.1177/0309133314548886

Pemberton, M. (1988). Soil erosion between Birchs Inlet and Elliott Bay, southwestern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, *122*(2), 109–114.

Pemberton, M. (1989). *Land systems of Tasmania. Region 7, South west*. Tasmania, Australia: D. O. Agriculture, Department of Agriculture.

Prentice, L. C. (1978). Modern pollen spectra from lake sediments in Finland and Finnmark, north Norway. *Boreas*, *7*(3), 131–153. https://doi.org/10.1111/j.1502-3885.1978.tb00271.x

R Development Core Team (2014). *R: A language and environment for statistical computing*, edited. Vienna, Austria: R Foundation for Statistical Computing.

Robbins, J. A., & Edgington, D. N. (1975). Determination of recent sedimentation rates in Lake Michigan using Pb-210 and Cs-137. *Geochimica et Cosmochimica Acta*, *39*(3), 285–304. https://doi.org/10.1016/0016-7037(75)90198-2

Saldaña, A. O., Hernández, C., Coopman, R. E., Bravo, L. A., & Corcuera, L. J. (2010). Differences in light usage among three fern species of genus Blechnum of contrasting ecological breadth in a forest light gradient. *Ecological Research*, *25*(2), 273–281. https://doi.org/10.1007/s11284-009-0656-8

Saros, J. E., & Anderson, N. J. (2015). The ecology of the planktonic diatom Cyclotella and its implications for global environmental change studies. *Biological Reviews*, *90*(2), 522–541. https://doi.org/10.1111/brv.12120

Saros, J. E., Stone, J. R., Pederson, G. T., Slemmons, K. E. H., Spanbauer, T., Schliep, A., et al. (2012). Climate-induced changes in lake ecosystem structure inferred from coupled neo-and paleoecological approaches. *Ecology*, *93*(10), 2155–2164. https://doi.org/10.1890/11-2218.1

Saunders, K. M., Harrison, J. J., Hodgson, D. A., Jong, d. R., Mauchle, F., & McMinn, A. (2013). Ecosystem impacts of feral rabbits on World Heritage sub-Antarctic Macquarie Island: A palaeoecological perspective. *Anthropocene*, *3*, 1–8. https://doi.org/10.1016/j.ancene.2014.01.001

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., et al. (2009). Early-warning signals for critical transitions. *Nature*, *461*(7260), 53–59. https://doi.org/10.1038/nature08227

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution*, *18*(12), 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Scheffer, M., Carpenter, S. R., Lenton, T. M., Bascompte, J., Brock, W., Dakos, V., et al. (2012). Anticipating critical transitions. *Science*, *338*(6105), 344–348. https://doi.org/10.1126/science.1225244

Schulz, M., & Stattegger, K. (1997). SPECTRUM: Spectral analysis of unevenly spaced paleoclimatic time series. *Computers & Geosciences*, *23*(9), 929–945. https://doi.org/10.1016/S0098-3004(97)00087-3

Seddon, A. W. R., Cole, L. E., Morris, J., Fletcher, M. S., & Willis, K. J. (2016). EcoRe3- Resistance, Recovery and Resilience of Long-term Ecological Systems. In *PAGES Magazine*, edited (75 pp.). https://doi.org/10.22498/pages.24.2.75

Simpson, G. L., & Anderson, N. J. (2009). Deciphering the effect of climate change and separating the influence of confounding factors in sediment core records using additive models. *Limnology and Oceanography*, *54*(6part2), 2529–2541. https://doi.org/10.4319/lo.2009.54.6_part_2.2529

Simpson, G. L., & Birks, H. J. B. (2012). Statistical learning in palaeolimnology. In H. J. B. Birks, et al. (Eds.), *Tracking environmental change using lake sediments: Data handling and numerical techniques* (pp. 249–327). Netherlands: Springer. https://doi.org/10.1007/978-94-007-2745-8_9

Simpson, G. L., & Oksanen, J. (2016). Package: analogue. In *Analogue and Weighted Averaging Methods for Palaeoecology*, edited.

Siteur, K., Eppinga, M. B., Doelman, A., Siero, E., & Rietkerk, M. (2016). Ecosystems off track: Rate-induced critical transitions in ecological models. *Oikos*, *125*(12), 1689–1699. https://doi.org/10.1111/oik.03112

Styger, J., & Kirkpatrick, J. B. (2015). *Less than 50 millimetres of rainfall in the previous month predicts fire in Tasmanian rainforest*. Paper presented at Papers and Proceedings of the Royal Society of Tasmania.

Sugita, S. (1993). A model of pollen source area for an entire lake surface. *Quaternary Research*, *39*(02), 239–244. https://doi.org/10.1006/qres.1993.1027

Townsend, S. A., & Douglas, M. M. (2000). The effect of three fire regimes on stream water quality, water yield and export coefficients in a tropical savanna (northern Australia). *Journal of Hydrology*, *229*(3-4), 118–137. https://doi.org/10.1016/S0022-1694(00)00165-7

Tyler, P. A. (1974). Limnological studies. In W. D. Williams (Ed.), *Biogeography and ecology in Tasmania* (pp. 29–61). The Hague, Dordrecht, Netherlands: Dr. W. Junk b.v. https://doi.org/10.1007/978-94-010-2337-5_4

Vanhoutte, K., Verleyen, E., Vyverman, W., Chepurnov, V., & Sabbe, K. (2004). The freshwater diatom genus Kobayasiella (Bacillariophyta) in Tasmania, Australia. *Australian Systematic Botany*, *17*(5), 483–496. https://doi.org/10.1071/SB03035

Vyverman, W., Vyverman, R., Rajendran, V. S., & Tyler, P. (1996). Distribution of benthic diatom assemblages in Tasmanian highland lakes and their possible use as indicators of environmental changes. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 493–508. https://doi.org/10.1139/f95-220

Wang, R., Dearing, J. A., Langdon, P. G., Zhang, E., Yang, X., Dakos, V., & Scheffer, M. (2012). Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature*, *492*(7429), 419–422. https://doi.org/10.1038/nature11655

Weckström, K., Weckström, J., Yliniemi, L. M., & Korhola, A. (2010). The ecology of Pediastrum (Chlorophyceae) in subarctic lakes and their potential as paleobioindicators. *Journal of Paleolimnology*, *43*(1), 61–73. https://doi.org/10.1007/s10933-009-9314-y

Whitlock, C., & Larsen, C. (2001). Charcoal as a fire proxy. In J. P. Smol, H. J. B. Birks, & W. M. Last (Eds.), *Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal, and siliceous indicators* (pp. 75–97). Dordrecht, Netherlands: Kluwer Academic.

Willis, K. J., Bailey, R. M., Bhagwat, S. A., & Birks, H. J. B. (2010). Biodiversity baselines, thresholds and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution*, *25*(10), 583–591. https://doi.org/10.1016/j.tree.2010.07.006

Wood, S. (2016). *Package: mgcv, in Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation*, edited.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Statistical Methodology Series B*, *73*(Part 1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wood, S. W., & Bowman, D. M. J. S. (2012). Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology*, *27*, 13–28. https://doi.org/10.1007/s10980-011-9677-0

Yee, T. W., & Mitchell, N. D. (1991). Generalized additive models in plant ecology. *Journal of Vegetation Science*, *2*(5), 587–602. https://doi.org/10.2307/3236170

Erratum

In the originally published version of this article, several instances of text were incorrectly typeset. The following have since been corrected and this version may be considered the authoritative version of record.

Section 1. Introduction, 1st paragraph: "Once a state shift has occurred in response to a perturbation, internal feedbacks can “fix” the ecosystem in the new stable state irrespective of continued perturbation—that is hysteresis (Fletcher et al., 2014; Scheffer et al., 2009; Scheffer & Carpenter, 2003).” was changed to “Once a state shift has occurred in response to a perturbation, internal feedbacks can “fix” the ecosystem in the new stable state irrespective of continued perturbation—i.e. hysteresis (Fletcher et al., 2014; Scheffer et al., 2009; Scheffer & Carpenter, 2003).”

Section 1. Introduction, 1st paragraph: “While theory predicts that EWS should precede some types of critical transitions detecting these signals empirically remains challenging, particularly for ecosystems with long generational timespans, such as temperate forests.” was changed to “While theory predicts that EWS should precede some types of critical transitions detecting these signals remains challenging, particularly for ecosystems with long generational timespans, such as temperate forests.”

Section 1. Introduction, 2nd paragraph: “A slowdown in recovery time as a system approaches a critical transition is termed “critical slowing down” (Scheffer et al., 2009), and it is this property that has received most attention when attempting to measure changes in resilience and detecting EWS (Scheffer et al., 2009; Wang et al., 2012).” was changed to “A slowdown in recovery time, as a system approaches a critical transition, is termed “critical slowing down” (Scheffer et al., 2009). It is this property that has received most attention when attempting to measure changes in resilience and detect EWS (Scheffer et al., 2009; Wang et al., 2012).”

Section 1.1. Biogeography of Tasmania, 1st paragraph: “The island is bisected by northwest-southeast trending mountain ranges that intercept the prevailing midlatitude westerly airflow, resulting in a steep west to east orographic precipitation gradient.” was changed to “The island is bisected by northwest-southeast trending mountain ranges that intercept the prevailing mid-latitude westerly airflow, resulting in a steep west to east orographic precipitation gradient.”

Section 1.1. Biogeography of Tasmania, 1st paragraph: “In the west, this has resulted in a failure of rain forest to occupy its climatic niche, and instead the landscape is dominated by fire-promoting plant communities.”

was changed to "In the west, this has resulted in a failure of rain forest to occupy its climatic niche, and instead, the landscape is dominated by fire-promoting plant communities."

Section 2.1. Coring and Chronology, 1st paragraph: "and pretreated in HCl to remove of any carbonates." was changed to "and pretreated with HCl to remove of any carbonates."

The four citations "Fletcher, Wolfe, et al., 2014" found in Section 4.1 and Section 4.2.2 were changed to "Fletcher et al., 2014".

Section 4.2.1. The Acquatic System, 1st paragraph: "While ROC is a measure of how rapidly a system state deviates from a stable steady state in response to a perturbation or a change in external conditions; with critical transitions, ROC increases when a system is unable to cope with the rapid changes (i.e., above some critical ROC threshold) and recovery slows (Dakos et al., 2012; Lim & Epureanu, 2011; Scheffer et al., 2009, 2012; Siteur et al., 2016)." was changed to "While ROC is a measure of how rapidly a system state deviates from a stable steady state in response to a perturbation or a change in external conditions. With critical transitions, ROC increases when a system is unable to cope with the rapid changes (i.e., above some critical ROC threshold) and recovery slows (Dakos et al., 2012; Lim & Epureanu, 2011; Scheffer et al., 2009, 2012; Siteur et al., 2016)."

Section 4.2.2. The Terrestrial System, 1st paragraph: "Despite marked changes in the Lake Vera aquatic ecosystem driven by burning of the local catchment, the pollen from Lake Vera show a degree of complacency to fire (Figures 6e–6h)." was changed to "Despite marked changes in the Lake Vera aquatic ecosystem driven by burning of the local catchment, the pollen from Lake Vera shows a degree of complacency to fire (Figures 6e–6h)."

Section 4.2.2. The Terrestrial System, 1st paragraph: "It is important to note that the source area airborne pollen into a lake is often considerably larger than the local lake catchment (Bunting et al., 2004; Prentice, 1978; Sugita, 1993)." was changed to "It is important to note that the source area of airborne pollen into a lake is often considerably larger than the local lake catchment (Bunting et al., 2004; Prentice, 1978; Sugita, 1993)."

Section 4.2.2. The Terrestrial System, 2nd paragraph: "We interpret this suite of changes in the terrestrial system as reflecting the cumulative effect of repeated fires on the resilience of this rain forest system via an opening of the canopy and an invasion by fire-promoting species, thus increasing the probability of future burning and the localized rain forest extinction (sensu; Fletcher, Wolfe, et al., 2014; Fletcher, Wood, & Haberle, 2014)." was changed to "We interpret this suite of changes in the terrestrial system as reflecting the cumulative effect of repeated fires on the resilience of this rain forest system via an opening of the canopy and an invasion by fire-promoting species, thus increasing the probability of future burning and localized rain forest extinction (sensu; Fletcher et al., 2014; Fletcher, Wood, & Haberle, 2014)."